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NEIGHBORHOOD INCOME, LANDSCAPE, AND LOCAL FACTORS RELATE TO DIFFERENCES IN POLLINATOR BIODIVERSITY IN DENVER CITY PARKS

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ABSTRACT

NEIGHBORHOOD INCOME, LANDSCAPE, AND LOCAL FACTORS RELATE TO DIFFERENCES IN POLLINATOR BIODIVERSITY IN DENVER CITY PARKS

Urbanization is a growing influence on pollinator species worldwide, benefiting some species while threatening others. Urban areas have high cover of impervious surfaces, inconsistent access to floral resources, and competition from non-native honeybees. Urban areas can also be impacted by a “luxury effect”, where greater biodiversity is found in more affluent areas. Despite these threats, city parks could be a crucial refuge for pollinator biodiversity. In this study, we investigated how pollinator species richness and community composition differed across Denver city parks depending on landscape-level factors, (neighborhood income and land cover surrounding a park), and local factors, (floral traits and honeybee abundance). After visiting 25 city parks three times during the summer of 2023, we found that income did not strongly relate to wild bee species richness or community composition, but floral species richness and origin did. We found that lower-income parks had a higher proportion of non-native weedy plants and lower wild bee species richness than parks with primarily native plantings. Wild bee communities differed in parks with high compared to low honeybee abundances, with more bumble bees observed in higher honeybee parks. Increased cover of impervious surfaces and income negatively related to butterfly species richness, but butterfly communities remained similar across parks. These findings suggest that managers can implement diverse native plantings in parks to support biodiverse pollinator communities regardless of neighborhood income level.

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CHAPTER 1: NEIGHBORHOOD INCOME, LANDSCAPE, AND LOCAL FACTORS RELATE TO DIFFERENCES IN POLLINATOR BIODIVERSITY IN DENVER CITY PARKS

1.1 Introduction

Urban areas are increasing exponentially to accommodate the world's growing human population (Ritchie et al., 2024), creating novel consequences for plants and animals (Vaz et al., 2023). Urbanization increases the cover of impervious surfaces and built infrastructure (Wu, 2014), creating barriers between greenspaces and reducing habitat for animals (Ayers and Rehan, 2021). Moderate urbanization can increase the species richness of many plants and animals (McKinney, 2008), but the most diverse and abundant class of animals on the planet, insects, have highly variable responses to urbanization (Wagner et al., 2021; Vaz et al., 2023). Cities support people and wildlife by creating parks, but their management can either help or harm insects. City parks can create beneficial insect habitat by planting native grasses and flowering plants. Alternatively, managers often plant lawn grass, non-native ornamental plants, and remove weedy plants with herbicides, limiting the insect species who can survive (McKinney, 2008). The resultant complexity of urban environments can either deter insects or support their growth, making urbanization a complex driver of insect population change worldwide (Cardoso and Gongcalves, 2018; Piano et al., 2020; Wagner et al., 2021).

Socioeconomic status shapes urban landscapes beyond land cover features. Research across animal groups suggests that urban areas display a “luxury effect” where greater biodiversity is found in areas of higher income (Leong et al., 2018). The luxury effect has been well investigated in birds, (Lerman & Warren, 2011; Chamberlain et al., 2019), with conflicting results depending on the intensity of urbanization. Chamberlain et al. (2019) found that the luxury effect held in less urbanized South African neighborhoods, where bird species richness was higher in wealthier areas. The opposite pattern was observed in extremely urbanized systems, with decreased bird species richness in wealthier neighborhoods (Chamberlain et al., 2019). Given the mosaic of urbanization intensity throughout cities and the higher cost of living in both the city center and near city parks, these nuances are important to consider in predicting the strength and direction of the luxury effect. Research must expand to understand if the luxury effect impacts other organisms to create equitable city planning and effective urban biodiversity conservation.

Urbanization is a primary driver of declines in pollinating insects, specifically native bees and butterflies (Armstead et al., 2024). These declines raise alarm because of the overwhelmingly positive impact of pollination services on food security and the biodiversity of native flora and fauna (Youngsteadt and Keighron, 2023). Butterflies also serve an important role as both avian food in their larval stage (Burghardt et al., 2009), and charismatic insect species that draw human interest and research funding in their adult (National Fish and Wildlife Foundation, n.d). Species richness of wild bees and butterflies can be lower in urban areas than in surrounding natural areas (Piano et al., 2020; Wenzel et al., 2020), but many species thrive in cities, making it imperative to understand what factors influence urban pollinators.

Urban areas host a complex mixture of local and landscape scale factors that impact pollinator communities and their management. Locally, vegetation type, microclimate, floral resources, and the presence of non-native insects like honeybees at a given location can influence pollinators (Ayers & Rehan, 2021). These are factors that park managers in urban areas often influence. On the landscape scale, the natural and built environment surrounding a park, such as the turf grass and cover of impervious surface, can impact wild bee and butterfly diversity (Luppi et al., 2018; Quistberg et al., 2016). Park managers typically cannot alter these landscape-scale factors. Thus, park management locally influences pollinators, while the impact of neighboring yards and impervious surface cover may increase or decrease the diversity of pollinator species found in a park depending on their foraging range and nesting requirements.

Differences in the life history traits of wild bee species make them more or less vulnerable to the effects of urbanization. Solitary bees require floral resources throughout the growing season, nesting locations such as loose bare ground and hollow cavities, and overwintering locations with woody debris, all lacking factors in urban environments (Danforth et al., 2019). Solitary bees are also limited by relatively short foraging distances, ranging from 200m-1000m, forcing them into an energetic tradeoff between relying only on nearby floral resources or stretching their foraging distance to find more food, risking energy expenditure that can decrease reproductive success (Zurbuchen et al., 2010). Contrary to solitary wild bees, bumble bees live in social colonies but they share many of the same foraging and nesting requirements (Goulson, 2010). Due to their larger bodies, bumble bees can travel farther to forage, but consequently require more food. Solitary and social bees can have a generalized or specialized diet depending on their proboscis length and range (Goulson, 2010). As a result of these life history differences, the pressures of urbanization disproportionately impact smaller-bodied, solitary, and specialist bee species (Ayers & Rehan, 2021), while generalist and large-bodied bee species experience fewer declines (Deguines et al., 2016; Ayers & Rehan, 2021).

Butterflies, like bees, have varied life history strategies among species, with certain traits proving more beneficial in urban environments. Butterflies have drastically different foraging distances across species, with only a handful of species documented (Scott, 1975; Auckland et al., 2004), but daily movement can be estimated between 500-1000m. While bees can have specialized diets and nesting requirements as adults, adult butterflies tend to be more generalist, but the larvae often rely on specific host plants (Rivest and Kharouba, 2024). However, some butterflies are more generalist as larvae, which are more common in some urban areas (Rivest and Kharouba 2024), suggesting that urbanization may drive out more specialist butterflies. Homogenized insect communities may be more vulnerable to decline (Wenzel et al., 2020), therefore understanding the life history traits and external influences that drive pollinators to succeed or decline in cities is essential to supporting long-term biodiversity.

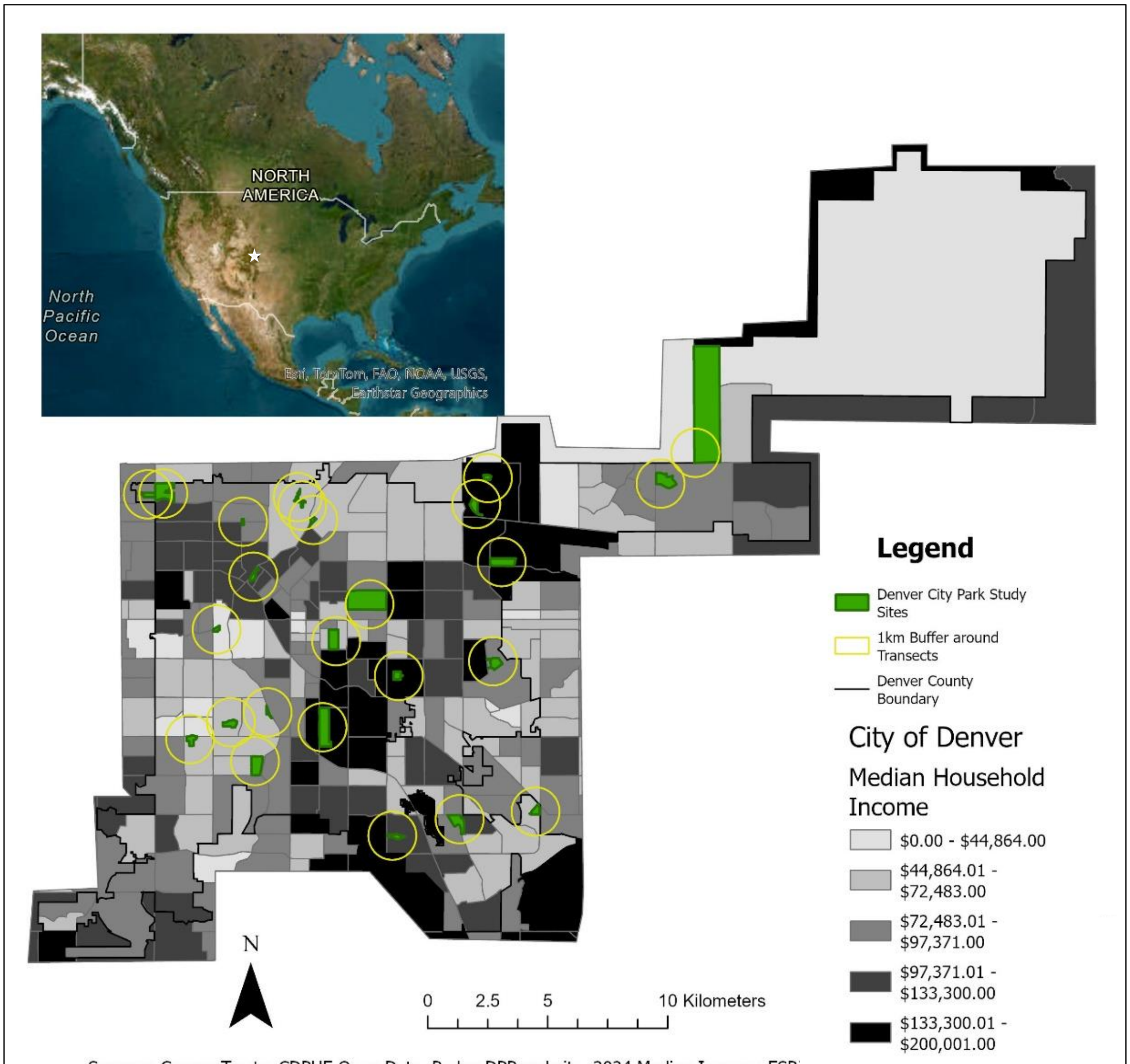
The complex relationship between income, local, and landscape-scale factors on pollinators is represented by the influence of urban European honeybees on wild bees. Honeybee keeping has recently increased drastically in urban areas (Lorenz and Stark, 2015), often inspired by misguided conservation efforts to support pollinators. Studies have demonstrated that honeybees directly outcompete small-bodied solitary bees (MacInnis et al., 2023), and bumble bees (Su et al., 2022), with adverse effects on bumble bee body size (Goulson & Sparrow, 2009). Most cities do not regulate honeybee keeping, thus the location and quantity of hives across cities are largely unknown. Urban honeybee keeping is, however, molded by the cost barrier to purchase and keep bees, and yard space to place hives. These factors suggest that more affluent neighborhoods may have more honeybees. The unchecked increase in urban honeybees has created an unforeseen competitive threat to native bees that may be more drastic in affluent than lower-income areas (Su et al., 2022), motivating us to research how honeybees foraging in city parks impact wild bee diversity.

Evidence suggests that local influences may impact bees and butterflies more than the surrounding landscape (Matteson & Langellotto, 2010; Williams & Winfree, 2013; Quistberg et al., 2016). However, little research has expanded to include income as an additional landscape factor. To inform park management, we investigated how local and landscape-level factors influence wild bee and butterfly species richness and community composition across 25 city parks in Denver, Colorado. Our objectives are to determine (1) what wild bees and butterflies are found in Denver city parks, (2) how income, landscape, and local factors relate to plant and pollinator diversity and shift community composition, and (3) how wild bee communities vary with honeybee abundance.

1.2 Materials and Methods

1.2.1 Site Selection

This study was conducted in 25 city parks managed by the Denver Parks and Recreation (DPR) department in Denver, Colorado (Figure 1). We visited each park three times, once in June, July and August of 2023. Parks varied in size (5 to 560 acres), vegetation composition, management intensity, and income level of the surrounding neighborhood. Parks were assigned neighborhood equity scores based on the Denver Parks and Recreation's Neighborhood Equity Index that assessed poverty rate, education level, proximity to parks, food access, access to medical care, morbidity, and mortality rate among other factors (Denver Department of Public Health and Environment, 2020). Scores ranged from 1-5, with 1 indicating the lowest inequity and 5 the highest (Denver Department of Public Health and Environment, 2020). We randomly stratified the order in which we visited parks by equity score and time of day to ensure minimal bias in the likelihood of pollinator detection for each park. Surveys were conducted between 0800 and 1800 in relatively sunny conditions with wind speeds below 10 mph, and a minimum temperature of 20 degrees Celsius (Dylweski et al., 2020).



Sources: Census Tracts: CDPHE Open Data, Parks: DPR website, 2024 Median Income: ESR

Figure 1. Map of study sites featuring the 25 parks in green, 1km buffers surrounding transect locations in yellow, a gradient of the median household income in Denver, CO neighborhoods, and a white star showing the relative location of Denver in North America. Denver County boundary is outlined in black.

1.2.2 Field Data Collection

To characterize sites, collect bees, and count butterflies we determined locations for two 100-meter-long transects at each park (Carrié et al. 2018). We intentionally placed transect locations in areas of dense floral resources during sampling to ensure the greatest likelihood of encountering pollinators, particularly bees (Hamblin et al., 2018). When possible, we placed transects in cultivated areas with planted floral resources. In most locations, cultivated areas did not span a 100m distance, therefore we included lawn grass and areas of non-cultivated plantings. We used these criteria during each visit to determine transects for pollinator and floral surveys. All transects were recorded using the application Gaia for spatial analysis.

We collected bees in hand-held insect nets. During each survey, two researchers slowly meandered the transect for 15 minutes, using a stopwatch to keep time, and captured all wild bees encountered with a net, pausing the timer during insect handling. Upon capture, we recorded what flower they were visiting. We targeted all bees for capture during sampling except queen bumble bees and honeybees. We identified queens to species by sight without capturing them. We quantified honeybees using a hand clicker during the 15-minute sampling period, then summed the values from both transects to provide a total for each park visit. After sampling, we stored the collected bees on ice and transferred them to a -20ºC freezer. Bees and any additional voucher specimens were pinned and identified using microscopes and various taxonomic keys (Supplement 1), and then identifications were verified by Colorado taxonomic experts. We determined whether species were generalist (polylectic) or more specialist (oligolectic) pollen foragers using keys listed in Supplement 2. Analysis describing "wild bees" includes all bee species except the European honeybee, and honeybee analyses are explicitly stated.

To count and identify butterflies, we conducted modified Pollard Walks (Pollard and Yates, 1993; Kral et al., 2018). All Pollard Walks were conducted by one person to ensure consistent identification skills and detection probability. Individuals not identifiable in the field were collected and identified later by an expert. Transects were walked at 20 meters per minute, recording any butterfly encountered within 2.5 meters on either side, 5 meters forward, and 5 meters above the ground. Each transect was repeated and spaced approximately 10 meters from the initial walk to yield the standard 10 minutes of sampling effort per Pollard walk. The modification of the traditional Pollard Walk into repeated transects was essential for consistent detection likelihood across parks that featured infrequent and dense floral resources, differing from the more uniform and heterogeneous landscape of natural areas that Pollard Walk methodology was originally designed for (Pollard and Yates, 1993). When possible, butterfly surveys occurred before bee surveys to limit disturbance and improve the likelihood of observing butterflies.

To identify floral species and relative abundance, one individual performed floral surveys at each park, ensuring consistent taxonomic skills and relative abundance estimations. Each floral species found within the transect area was identified using floral identification applications Seek by iNaturalist and PictureThis. Relative abundance was estimated for each flowering plant following the log10 bins approach outlined in Mola and Williams (2018) to represent the floral resource availability during each park visit. After observational collections, floral species were identified by origin using the USDA Plant Database (U.S. Department of Agriculture, Natural Resources Conservation Service, n.d.) and Colorado Plant Database (Jefferson County, Colorado, n.d.), to categorize species as “native” or “non-native” based on the recorded geographic native range and “cultivar” or “weedy” based on whether they were planted cultivars or established on their own.

1.2.3 Landscape Data Collection

To obtain and analyze landscape data, we used ArcGIS Pro version 3.2.1. Using layers from the City and County of Denver, we created a map of the parks, Denver County boundary, Denver census tracts, survey transect lines exported from Gaia, and Land Cover and Land Use layers from the Denver Regional Council of Governments. We calculated the mean coordinates of the transects at each park to represent survey locations and exported the coordinates as a point layer into ArcGIS Pro. We used the “Buffer” tool to create a 1km buffer around each point, then found the area of each land cover type (Table 1) within the buffer. We divided the area of each land cover feature by the buffer’s area to determine the feature’s relative cover surrounding a given park.

To calculate the luxury effect in Denver, we measured the median household income surrounding each park. We used the “Enrich Layer” tool, which drew from the ESRI Online Living Atlas, to determine the 2023 Median Income Values for the 1km buffered area surrounding each park. We chose the 1km buffer to obtain an adequate sample size of homes from the surrounding neighborhoods and for biological relevance to the pollinator community, consistent with Matteson and Langellotto (2010) and Youngsteadt and Keighron (2023).

1.2.4 Analysis

1.2.4.1 Summary of plant and pollinator communities in Denver Parks

To summarize pollinator and plant communities in Denver Parks we presented the total number of pollinators recorded, species richness, defined as the total number of unique species recorded at each park visit, species occurrence across parks, life history information corresponding to common and rare species, and common plant-pollinator interactions. We calculated species occurrence as the number of parks where a species was present divided by the total number of parks.

1.2.4.2 Income, local, and landscape factors related to pollinator species richness

To analyze the relationship between income, local factors, landscape factors, and pollinator diversity, we measured 16 variables that could influence bee and butterfly species richness, focusing on six local variables at the park level and 10 landscape variables at 1km surrounding each park (Table 1). We aimed to create a global Generalized Linear Mixed Effects Model (GLMM) featuring as many of our landscape and local variables as possible, but many factors were highly correlated, preventing model convergence. To address this, we used the ‘car’ package in RStudio to create a correlation matrix and plot and eliminated values with correlation coefficients above 0.7 (James et al., 2013; Kim, 2019). We also checked collinearity using VIF, eliminating values with VIF>5 (James et al., 2013). We used the scale function in R to standardize predictor variables.

Table 1. List of all local (within-park) and landscape factors measured in a 1km buffer surrounding each sampling area (n=25).

	Variable	Units
Local Factors (Measured At Site)	Honeybee Abundance	Number
	Floral Species Richness	Number
	Floral Abundance	Number, Log Abundance
	Floral Origin (Weedy/Native/Cultivar)	Proportion
Landscape Factors (1km Buffer)	Median Household Income	Number ($)
	Impervious Surface Cover	Proportion
	Structures	Proportion
	Irrigated Turf	Proportion
	Scrubland	Proportion
	Tree Canopy	Proportion
	Water	Proportion
	Grassland/Prairie	Proportion
	Barren Rock	Proportion
	Cropland	Proportion

To explain variance in species richness of wild bees across parks, we constructed a GLMM with 9 fixed effects: floral species richness, the proportion of weedy, cultivar, and native plant, honeybee abundance, cover of impervious surface, barren rock, scrubland, and irrigated turf, and median household income, with park name as a random effect to account for repeated visits. To explain variance in butterfly species richness, we constructed a GLMM with 7 fixed effects relevant to butterfly life history: floral species richness, total floral abundance, impervious surface cover, irrigated turf cover, scrubland cover, tree canopy cover, and median household income with park name as a random effect. All GLMMs were developed using a Poisson adjustment. We ran models of all combinations of the predictors and used the Akaike Information Criterion (AIC) to identify the most parsimonious model. GLMMs were assessed for normality using residual plots. To assess the explanatory strength of our models on pollinator richness, we calculated marginal and conditional R^2 values using the “delta” method and used ANOVA to assess the statistical significance of each variable. We calculated and presented partial R^2 values using the ’sensemakr’ package for all predictor variables present in GLMMs with ΔAIC less than 2, representing models with strong support.

1.2.4.3 Variance in floral communities related to wild and honey bees

Due to the high collinearity of many variables in our GLMMS and the importance of floral resources to bee species richness, we performed additional analysis to assess how income influenced floral communities and the impact of floral abundance and origin on wild and honey bees. We compared the community composition of flowering plant species across parks by median income using permanova. Comparing communities accounted for the relative abundance of each species observed in a park rather than only the number of species. We interpreted community differences as shifts in both the species observed and the frequency of encountering each species across parks. We created a linear model (LM) to analyze the relationship between median income and the proportion of weedy flowering plants across parks. To understand how a high proportion of weedy flowering plants impacted wild bee richness and honeybee abundance directly, we created two additional LMs. To understand how the abundance of flowing plants impacted honeybee abundance, we created a final LM comparing floral abundance with honeybee abundance. All LM used a Poisson adjustment to account for abundance metrics, and we present R^2 and p values with significance at $\alpha<0.05$.

1.2.4.4 Income, local, and landscape factors related to pollinator communities

To analyze shifts in wild bee and butterfly communities by local and landscape variables, we performed non-metric multidimensional scaling (nMDS). Using the ‘vegan’ package in R, we calculated bee and butterfly relative abundance using the “total” method, then calculated the Bray-Curtis dissimilarity for communities at each park. We developed categorical variables to address how median household income, floral origin, impervious surface cover, and honeybees influenced pollinator communities and performed permanova tests to determine the statistical significance of each relationship. We compared community differences for the wild bee nMDS based on median income and floral origin to assess the influence of the luxury effect and high proportions of native flowering plants on wild bee communities. We compared butterfly communities by impervious surface cover and median income to assess the luxury effect and influence of urbanization on butterfly communities. We summarized differences among communities by presenting changes in generic and species richness.

To define the categories, we consulted the literature and used natural breaks in the dataset. Low income for a one-person household is defined as roughly $62k in Denver, CO (U.S. Department of Housing and Urban Development, 2022) but few parks fell below that level, likely due to the inherently higher home value in areas surrounding parks. We expanded "low" income to include a median income below $80k, still deemed low income for a family of three, and "high" income as greater than $80k to better represent the range of income levels surrounding parks (U.S. Department of Housing and Urban Development, 2022). To calculate floral origin, we categorized the floral species observed at each park as weedy, native, or non-native cultivars. Then, we summed the total inflorescences for each group and divided by the park's total inflorescences. Each park was identified by the floral category with the highest proportion in the park. High and low impervious surface cover was split above and below 35% to represent the relative midpoint of the dataset. Honeybee quantities over 250 were categorized as "high", and below 250 as "low", creating an adequate sample size to keep nMDS stress below 0.2 following examples from MacInnis et al. (2023). Parks designated as high honeybee had a range of 1315 compared to only 229 for low honeybee parks, indicating a rapid increase in honeybee abundance in parks with more than 250 observed honeybees.

1.2.4.5 Wild bee community differences in parks with varied honeybee abundance

To further understand how wild bee communities shifted due to honeybee influence and urbanization, we performed an ordination and compared community shifts visually using a dot chart. The nMDS ordination compared the relative abundance of wild bee communities at parks with high and low honeybee abundance, and differences were analyzed with permanova. To create the dot chart, we grouped wild bee observations into high and low honeybee groups and plotted the relative abundance of the wild bee genera in each group. We analyzed differences using permanova. To understand how the life history traits of individual bee species may impact their relative abundance in Denver parks, we plotted an nMDS with all observed wild bee species categorized by diet specialization and relative abundance and used a permanova statistical test to assess differences.

1.3 Results

1.3.1 Summary of plant and pollinator communities in Denver Parks

From 75 completed surveys, we collected 3199 total wild bees from 143 species and observed 1165 butterflies from 37 species (Supplemental Tables 1 and 2). Of the 143 bee species, 36 were first-time records in the county of Denver. The most common observations were *Bombus fervidus* (362) at 100% of parks, and *Halictus ligatus* (341) observed at 96% of parks, both common species across North America. Alternatively, we recorded 3 observations of *Bombus occidentalis,* a species previously common in Colorado with recently documented declines (Janousek et al., 2023). The most frequently observed butterflies were *Pieris rapae* (262), at 100% of parks, and *Burnsius communis* (229), at 92% of parks. We recorded 8108 honeybees across all visits, with the most observations occurring in Washington Park (1,565), and the fewest at First Creek at DEN Open space (21). Of the 331 species of flowering plants observed, wild bees interacted with 152 (Supplemental Table 3), 36.2% were native, with 20.4% described as weedy and 43.4% as non-native cultivars. The most common bee-plant interactions were on non-native flowers: *Trifolium repens* (n=203) and *Melilotus officinalis* (n=174), and similarly for butterflies, *Trifolium repens* (n=34) and *Taraxacum officinalis* (n=23).

1.3.2 Income, local, and landscape factors related to pollinator species richness

The most parsimonious model for wild bee species richness included floral species richness as the sole predictor variable (R^2_{mar}: 0.308, R^2_{con}: 0.532; Table 2), the only statistically significant predictor variable (*p*=0.004). Adding household income did not strongly improve the model's predictive capability (R^2_{mar}: 0.268, R^2_{con}: 0.519; Table 2). The low delta AIC among models indicates the strong influence of floral species richness on wild bee species richness, and the influence of every predictor variable to explain some variation in wild bee species richness (Table 2). In the global model with all predictor variables included, the partial R^2 for floral species richness explained 10.2% of the variance in wild bee species richness (Fig. 2). The second most influential variable was honeybee abundance, which explained only 1.6% of the model's variance (Fig. 2).

Table 2. Butterfly species richness model output ranked by AIC showing all models with ΔAIC <2 indicating strong support. Variance is quantified by partial and marginal R^2.

Predictors	**delta**	**df**	**AIC**	**weight**	R^2_{mar}	R^2_{con}
Floral Species Richness	0.000	3	463.128	0.041	0.308	0.532
Floral Species Richness + Household Income	1.159	4	464.277	0.023	0.268	0.519
Floral Species Richness+ Honeybee Abundance	1.203	4	464.321	0.022	0.272	0.530
Floral Species Richness+ Cultivar Relative Abundance	1.342	4	464.459	0.021	0.269	0.528
Floral Species Richness + Barren Rock Prop	1.439	4	464.557	0.019	0.271	0.518
Floral Species Richness + Weedy Relative Abundance	1.500	4	464.615	0.019	0.269	0.511
Floral Species Richness + Scrubland Prop	1.580	4	464.697	0.019	0.266	0.520
Floral Species Richness + Irrigated Turf Prop	1.789	4	464.907	0.017	0.265	0.520
Floral Species Richness + Imp Surface Prop	1.903	4	465.021	0.016	0.263	0.520
Floral Species Richness + Honeybee Abundance + Barren Rock Prop	2.099	5	465.217	0.014	0.286	0.525

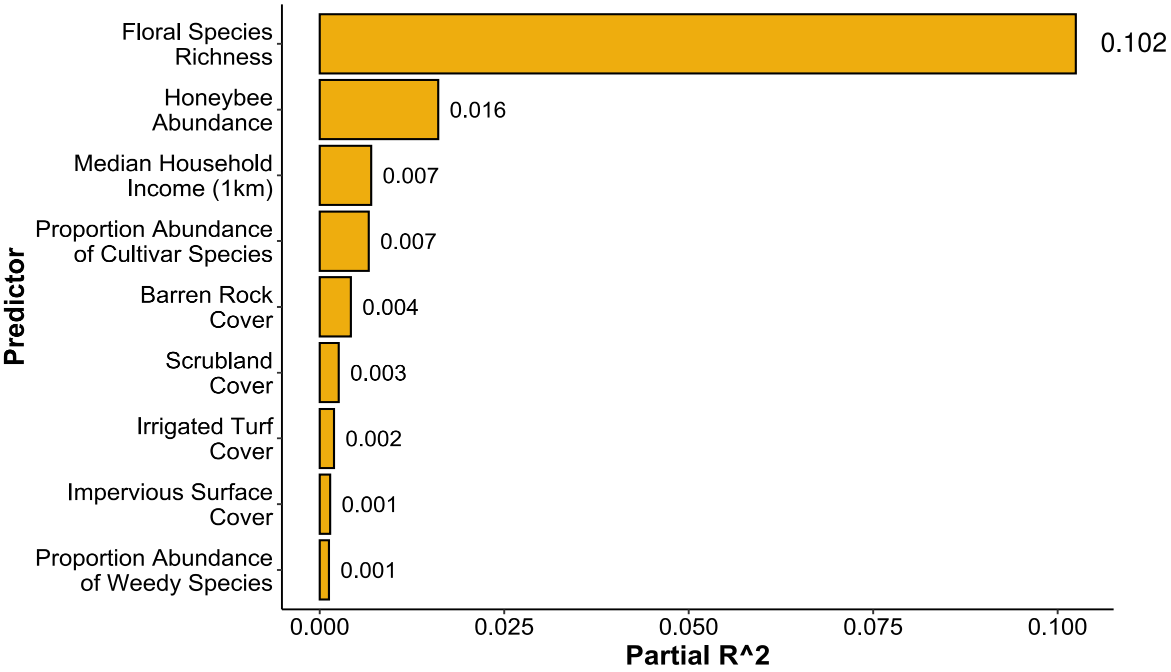


Figure 2. Bar graph representing the partial R^2 values for each predictor variable contributing to a wild bee GLMM with ΔAIC <2, indicating each variable that strongly explains variation in wild bee species richness with yellow bars.

The most parsimonious model for butterfly species richness included floral abundance impervious surface cover, and household income (R^2_{mar}: 0.168, R^2_{con}: 0.184; Table 3). Impervious surface cover (*p*=0.027) and household income (*p*=0.044) had significant negative relationships with butterfly species richness (Table 3). Delta AIC remained below 4 among the top 40 model combinations, indicating the explanatory strength of all measured predictor variables to explain variance in butterfly species richness. In the global model with all predictors included, impervious surface cover had the highest partial R^2, explaining 6.7% of the model's variance, and median household income explained 5.4% of variance (Fig. 3). All other variables explained 1% or less of variance (Fig. 3).

Table 3. Butterfly species richness model output ranked by AIC showing all models with ΔAIC <2 indicating strong support. Variance is quantified by partial and marginal R^2.

Predictors	delta	df	AIC	weight	R^2_{mar}	R^2_{con}
Floral Abundance + Imp. Surface + Household Income	0.000	5	335.330	0.079	0.168	0.184
Impervious Surface	0.831	3	336.161	0.046	0.091	0.219
Impervious Surface + Household Income	1.256	4	336.586	0.037	0.116	0.224
Floral Species Richness + Imp. Surface + Household Income	1.275	5	326.605	0.037	0.146	0.221
Floral Species Richness + Floral Abundance + Imp. Surface + Household Income	1.748	6	337.078	0.029	0.170	0.192
Floral Abundance+ Imp. Surface	1.801	4	337.131	0.028	0.106	0.198
Floral Abundance + Imp. Surface + Tree Canopy + Household Income	1.933	6	337.262	0.027	0.169	0.188
Floral Abundance+ Imp. Surface + Scrubland Prop + Household Income	1.945	6	337.274	0.026	0.169	0.185
Floral Abundance+ Imp. Surface + Irrigated Turf + Household Income	1.991	6	337.321	0.026	0.168	0.183
Floral Species Richness + Imp. Surface	2.124	4	337.454	0.024	0.102	0.216

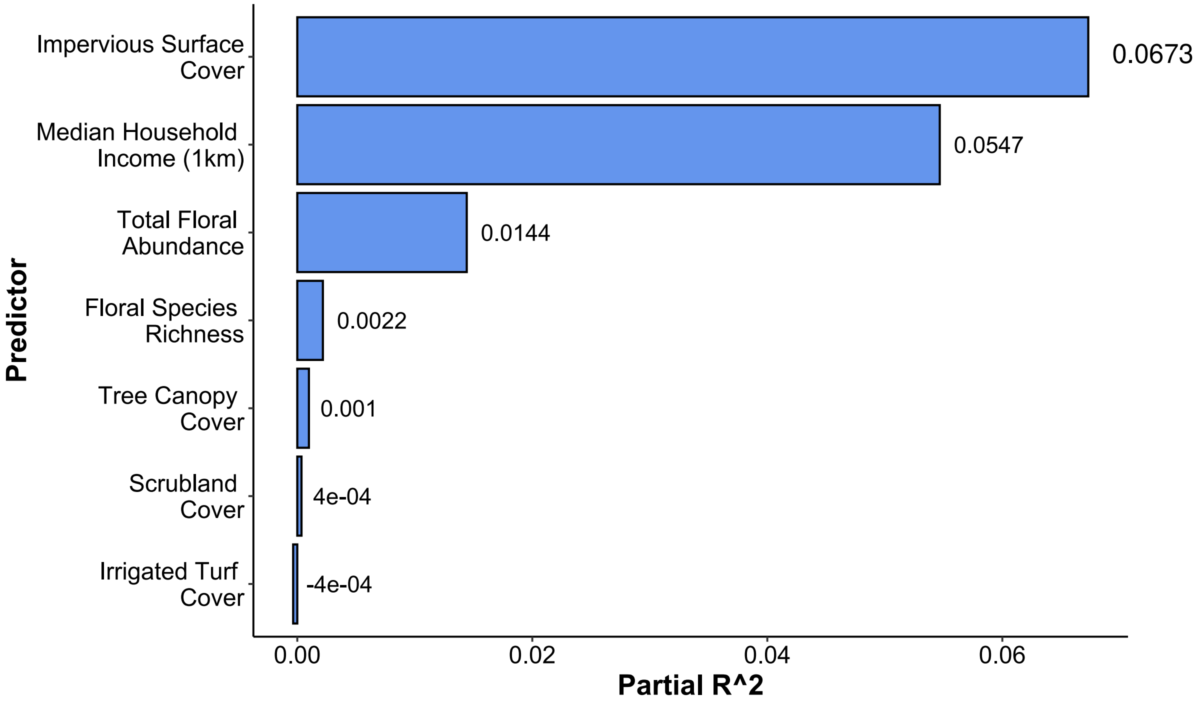


Figure 3. Bar graph representing the partial R^2 values for each predictor variable contributing to a butterfly GLMM with ΔAIC <2, indicating each variable that strongly explains variation in butterfly species richness with purple bars.

1.3.3 Variance in floral communities related to wild and honey bees

We found no significant differences among floral communities based on median neighborhood income (*p*=0.204), indicating a large spread in floral species composition and relative abundance across parks regardless of income. Income did impact floral origin (Figure 4A). We found significantly more flowering plant inflorescences designated “weedy” in parks surrounded by lower median income neighborhoods (*p*=0.014; Fig. 4A). Floral origin and abundance impacted both wild bees and honeybees. Significantly fewer wild bee species were found in parks with more weedy flowering plants (*p*=0.012; Fig. 4B). Honeybee abundance significantly increased with floral abundance (*p=9e-5*; Fig. 4C) but was not impacted by floral origin as weedy (*p=0.63*; Fig. 4D).

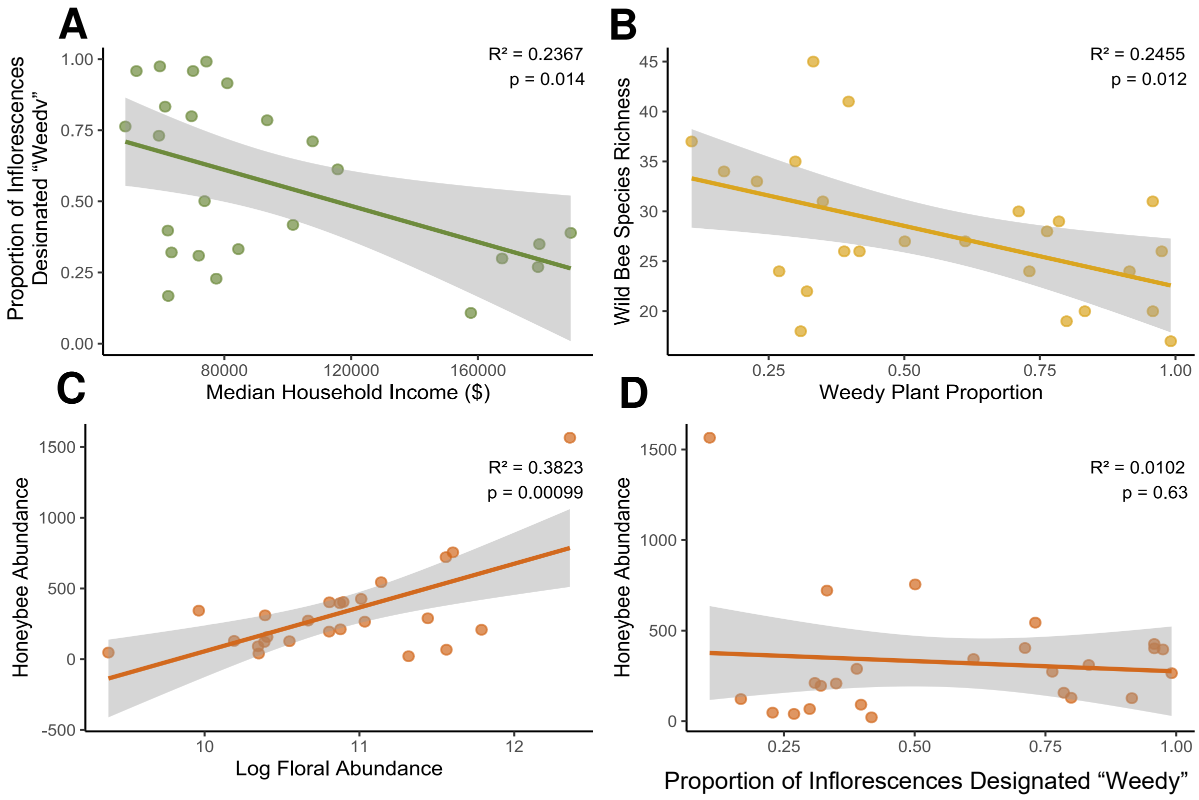


Figure 4. Linear model scatterplots representing the relationships between median neighborhood income in green (A) and weediness and wild bee species richness in yellow (B). Honeybees are represented by dark orange scatterplots, comparing honeybee abundance and floral abundance (C), and the proportion of weedy flowering plants and honeybee abundance (D).

1.3.4 Income, local, and landscape factors related to pollinator communities

We found significant differences among wild bee communities in parks with primarily weedy, native, or non-native cultivar flowering plants (p= 0.034; Fig. 5), but no clear differences in areas of high and low household income (p= 0.18; Fig. 5). In high-income parks, we recorded 93 wild bee species from 28 genera, compared to 101 species from 34 genera in lower income parks. Only one park had mostly cultivar flowering plants, and we recorded 26 bee species from 10 genera. In parks with mostly native flowering plants, we recorded 98 species from 32 genera, compared to 83 species from 29 genera in weedy parks. The stress value 0.18 indicates an acceptable fit for this ordination with minor distortion.

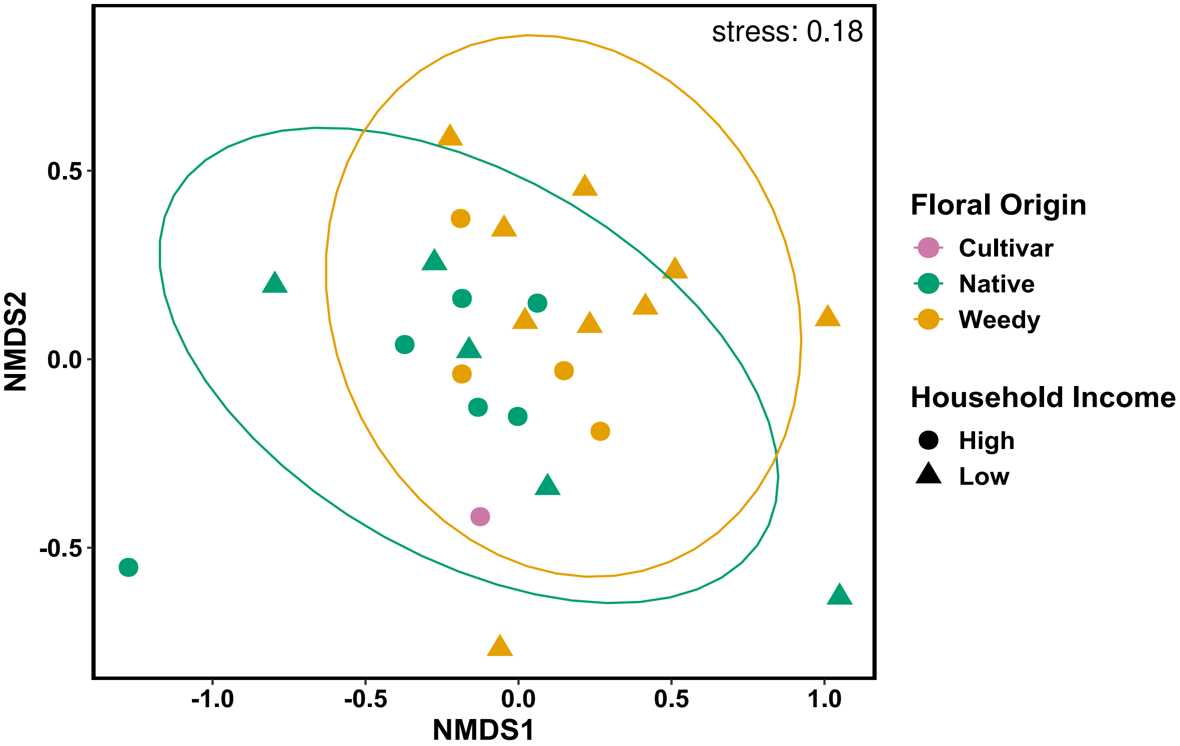


Figure 5: Non-metric multidimensional scaling (nMDS) plot based on Bray-Curtis dissimilarity of wild bee communities recorded in Denver Parks by high-income (>$80k) and low-income (=<$80k) neighborhoods and majority floral composition as cultivar, native, and weedy. High-income parks are represented by circles, and low as triangles. Colors represent the origin of most flowering plants in a park, with pink as cultivar, green as native, and yellow as weedy. Closer proximity among shapes represents parks that are more similar in wild bee species composition, and a larger distance between shapes represents less similar communities. Narrower ellipses reflect less variability among parks, suggesting a more homogeneous group.

We found no significant differences among butterfly communities based on the three most influential variables in our butterfly models: impervious surface cover (*p*= 0.132; Fig. 6), median income (*p*= 0.334; Fig. 6), or floral abundance (*p*=0.588). We found similar species richness in high-income parks (24) and low (28), but fewer species in high impervious surface cover parks (21) than those with lower impervious surface cover (30). The stress value 0.16 indicates an acceptable fit for this ordination with minor distortion.

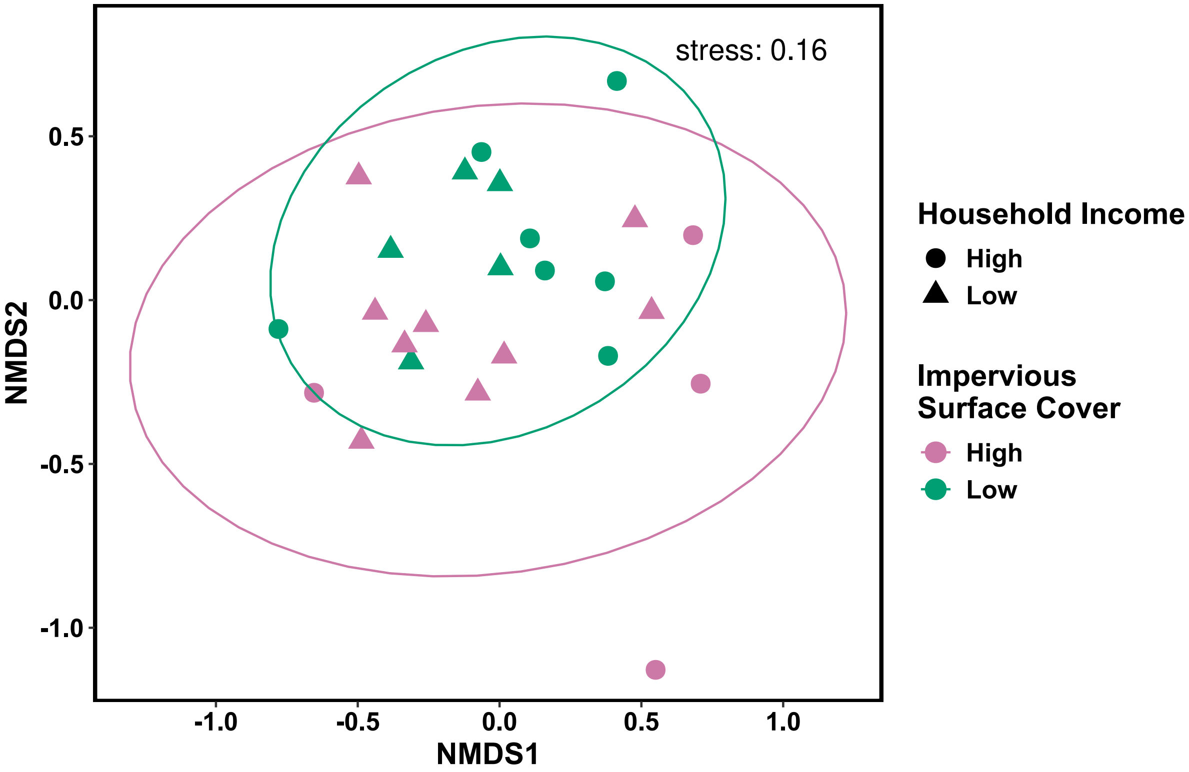


Figure 6. Non-metric multidimensional scaling (nMDS) plot based on Bray-Curtis dissimilarity from butterfly abundances recorded in Denver Parks with high (>$80k) or low (=<$80k) median neighborhood incomes, and high (>35%) or low (=<35%) surrounding impervious surface cover. High-income parks are represented by circles, and low as triangles. Pink represents high impervious cover surrounding a park, and green represents low. Each circle or triangle represents the community of butterfly species at each park. Closer proximity between shapes represents parks with more similar butterfly species composition, and a larger distance between shapes represents less similar communities. A narrower ellipse reflects less variability among parks, suggesting a more homogeneous group, while a wider ellipse indicates greater variability.

1.3.5 Wild bee community differences in parks with varied honeybee abundance

We found significant differences among wild bee communities in parks with high and low honeybee abundance (*p*=0.002, Fig. 7). The stress value of 0.18 indicates an acceptable fit for this ordination with minor distortion. We observed bees in the genus Bombus more often in high honeybee parks than in low honeybee parks (Supplemental Fig. 1) but found no statistically significant differences in the relative abundance of wild bee genera observed in high versus low honeybee parks (*p*=0.53). There were no significant differences in the richness of genera or species observed in high (31; 82) or low (32; 79) honeybee parks (Figure 8). We found that the most frequently collected wild bees and most species observed in Denver Parks were generalists, (polylectic; Supplemental Figure 1).

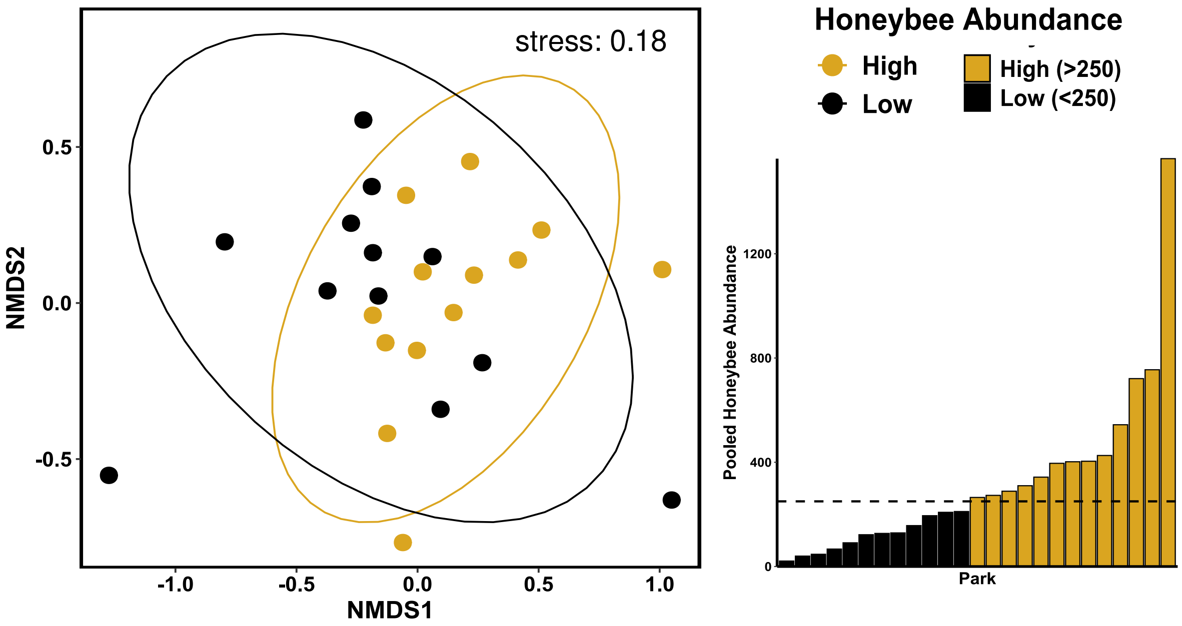


Figure 7. Non-metric multidimensional scaling (nMDS) plot based on Bray-Curtis dissimilarity from native bee relative abundances recorded in Denver Parks with high (>250) and low (=<250) honeybee abundances pooled over three visits. Yellow represents high honeybee abundance sites, and black represents low. Each circle represents the community of wild bee species at each park, and the closer proximity of circles represents parks with more similar wild bee species composition, and a larger distance between circles represents less similar communities. A narrower ellipse reflects less variability among parks, suggesting a more homogeneous group, while a wider ellipse indicates greater variability. Histogram represents the spread of honeybee abundance across the 25 parks.

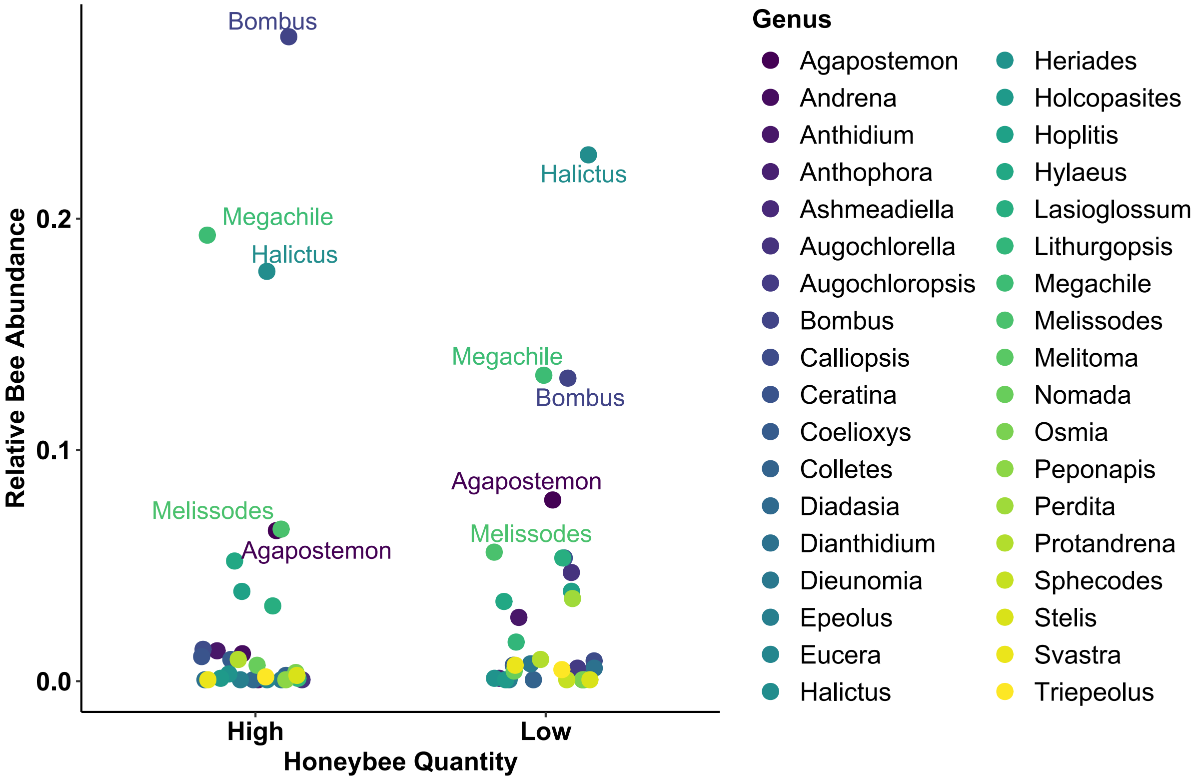


Figure 8. Dot chart comparing the relative abundance of each wild bee genus to understand the differences between wild bee communities in parks that have high or low honeybee abundance. Each color represents a unique wild bee genus. The abundance of each genus is compared to all other genera observed in high and low honeybee sites, with the relative abundance for all genera summing to 1. The five most abundant genera are labeled.

1.4 Discussion

Despite previous evidence that the luxury effect drives differences in arthropod species richness and community composition (Leong et al., 2018), we found that local and landscape factors such as floral species richness and land cover are the most influential drivers in Denver, Colorado parks. Higher neighborhood income had a weak negative association with wild bee and butterfly species richness and did not influence community composition. Floral species richness has been identified as a key supporter of bee population success (Neumann et al., 2024), and we found that higher-income areas did have fewer weedy non-native flowering plant species and resultantly greater bee species richness. Honeybees were also more common in parks with dense, but not necessarily species-rich, floral resources. This was associated with shifts in wild bee communities in high honeybee parks that best supported *Bombus* species and generalist foragers. Landscape factors were more strongly associated with changes in butterfly species richness than local floral factors. Higher cover of impervious surfaces and higher median income were both associated with lower butterfly species richness. Local factors may be more impactful for wild bees considering the importance of adult foraging during the growing season, whereas butterflies may be more tied to the landscape considering their reliance on specific host plants and larval herbivory (Burghardt et al., 2009).

Affluent parks generally featured greater proportions of native cultivars and fewer weedy flowers, but parks within each income level varied greatly. Neighborhood income and property taxes fuel city park management resources, creating inequity between funding for park management and resultant floral resource availability (Leong et al., 2018). Increased resources devoted to management may explain the greater bee species richness found in parks with fewer weedy species, but often these well-managed parks featured extensive lawns and pesticide use (Leong et al., 2018; Siviter et al., 2023), thus creating a weak overall effect of neighborhood income on bee species richness in parks (Table 2). Low-income parks often had fewer floral resources or a greater proportion of weedy species, thus allowing the weedy species to persist and support pollinators throughout the growing season. Neighborhood income was inversely related to butterfly species richness in our most parsimonious GLMM, suggesting that the luxury effect has a mixed influence on pollinators depending on their life history, and parks need complex habitats beyond floral resources to support diverse pollinators. Of the parks we studied in Denver, very few are deemed low-income by the Colorado Department of Health and Environment, potentially making the luxury effect more difficult to detect in Denver Parks (U.S. Department of Housing and Urban Development, 2022).

Greenspaces like parks are important biodiversity hubs, but lawns and gardens could be equally influential in supporting arthropod communities. To address the limitation of sampling only parks, we used a 1km land cover buffer surrounding each park to represent an accurate foraging distance for bees and butterflies. However, we found a very weak influence from surrounding land cover features in our models. Studies suggest that finer-scale landscape data may be needed to determine the influence of urban landscape drivers, particularly for butterflies (Matteson and Langellotto, 2010; Rivest and Kharouba, 2024). Measuring butterfly host plants is another key variable in predicting butterfly biodiversity that was not included in this study (Rivest and Kharouba, 2024). Including finer-scale vegetation data through both GIS and on-the-ground sampling could provide the missing details to create more explanatory models for butterfly species richness and differences in community composition. We included neighborhood land cover features and structural cover within our buffer but did not sample the floral resources outside of parks. We demonstrated that floral species richness was essential for supporting high wild bee species richness in urban parks, and including flowering plants from home lawns and community gardens could be an important next step for measuring wild bee diversity more completely, whether through community science or a low-impact trapping methodology.

The composition of the wild bee and butterfly communities may be shaped by factors different from those driving variance in species richness. We revealed that floral origin in a park significantly influenced wild bee community composition, whereas median income did not, despite the strong linear relationships between income, floral weediness, and wild bee species richness. Butterfly communities did not differ by median income, impervious surface cover, or floral abundance, which all drove variation in species richness. Pollinator community assemblage, therefore, may be more sensitive to factors like native floral origin, diverse microclimates, and rare host plants that are essential for specialist insects (Bergerot et al., 2011; Ayers & Rehan, 2021). Through this comparison, we see that different factors are associated with changes in species richness than shifts in community composition, illuminating the importance of including both metrics for a holistic diversity assessment. High species richness may not represent a stable community because few species are common while most are rare, making each park a unique host of insect diversity with specific habitat needs. Understanding the drivers of pollinator community composition is an important step toward the long-term conservation of urban pollinator diversity.

Honeybees impacted wild bee communities on a local scale regardless of neighborhood income. Urban beekeeping has risen in popularity recently, creating competition for foraging resources and pathogen spillover to native bees (Lorenz and Stark, 2015; MacInnis et al., 2023). Honeybees were ubiquitous in parks with high floral abundance (Fig. 3C), suggesting they could be more competitive with wild bee populations foraging on abundant but not diverse flower communities, often observed in our low-income parks. These findings are consistent with our ordination analysis, where we observed significantly different bee communities in parks with higher honeybee abundances. We also found that *Bombus* (bumble bee) species were more abundant in high than low honeybee parks, consistent with findings by MacInnis et al. (2023) who found that honeybees negatively impacted small bee diversity, but not larger-bodied bees like bumble bees. Goulson and Sparrow (2009) found that bumble bee body size decreased due to honeybee competition, suggesting that alternate methods to bee abundance, richness, and community composition should be explored to further understand honeybee competition. Honeybees are generalist foragers and there are currently no restrictions upon owning hives in Denver, so it is important to continue monitoring their influence in urban areas as their populations increase.

Life history traits shape pollinator communities in urban areas, and we can manage land to support diverse life history strategies that create diverse communities. Urbanization can create increased landscape heterogeneity, but evidence suggests insect communities may homogenize over time, with certain winners who can thrive in urban settings (Wenzel et al., 2020; Rivest and Kharouba, 2024). Of the over 1,000 bee species and 250 butterfly species in Colorado, we detected roughly 15% of those species in Denver. Our wild bee species ordination revealed that the most often observed bee species were generalist feeders, and the rarer species fell into more specialized feeding guilds. Our most frequently collected solitary species, *Halictus ligatus,* is a ground-nesting generalist feeder making it adaptable to urban systems. The same goes for our most observed butterfly, *Pieris rapae,* which oviposits on common Brassicaceae garden plants available in urban and rural areas alike. We observed very few individuals of most of our pollinators, emphasizing the importance of using alternate metrics to address the importance of rare specialist interactions in cities. Analyzing wild bee community shifts based on diet breadth was a useful first step, but future studies should move beyond foraging interactions to understand how urbanization impacts nesting, reproductive success, and overwintering.

1.5 Conclusion

We demonstrated the impacts of neighborhood income, landscape, and local factors in Denver, Colorado on wild bee and butterfly communities. Today’s human settlement and neighborhood income have been shaped by hundreds of years of urban development, and we can see the results of the luxury effect on park floral resources and management strategies that impact pollinator communities. We determined that local factors including floral species richness and native plantings improve butterfly and wild bee species richness and combat the potential influence of honeybee competition. Despite evidence that high floral species richness supports high pollinator richness (Neumann et al., 2024), many parks featured gardens with highly diverse non-native cultivars, but low pollinator activity. Studies suggest that non-native cultivars and weedy flowering plants support generalist pollinators, but only native floral species support the maximum diversity of wild bees with more specialized foraging preferences (Lowenstein et al., 2019; Seitz et al., 2020). Managers can support pollinator foraging by planting native flowering plants and grasses when possible and keeping weedy plants in lawn areas.

Studies across urban greenspaces provide evidence that biodiversity is supported by gardens (Matteson et al., 2008), residential yards (Lerman & Warren, 2011), and parks (Banaszak-Cibicka et al., 2018), but the influence of the urban landscape on biodiversity is highly variable by species. The pressure of urbanization may be filtering pollinator communities to overrepresent large wild bees, and generalist butterflies, functionally homogenizing communities and leaving them more vulnerable to decline. We found that landscape factors representative of urbanization may be more detrimental to butterfly communities than bees, making it important to provide local requirements for butterflies like specialized host plants. Urbanization will only intensify in the coming years, making it imperative to study the impacts of land use change on pollinators at various scales and create the best habitat possible in urban areas (Ballare et al., 2019; Rivest and Kharouba, 2024). Creating equitable park management across neighborhood income levels is one step toward environmental justice, promoting pollination services for people of all income levels, and conserving pollinator communities for generations.

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APPENDIX 1

A.1 Taxonomy Works Cited

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Table A1.1 Table of all wild bee species collected in Denver Parks organized by Family, Genus, and Species. Subgenera are indicated in the species column, and numbers indicate individuals that could not be identified to one species by taxonomic keys, but represented a common species agreed upon by experts.

Family	Genus	Species
Andrenidae	*Andrena*	*commoda*
Andrenidae	*Andrena*	*wilkella*
Andrenidae	*Andrena*	*hippotes*
Andrenidae	*Calliopsis*	*andreniformis*
Andrenidae	*Perdita*	*ignota*
Andrenidae	*Andrena*	*erythrogaster*
Andrenidae	*Andrena*	*nigrae*
Andrenidae	*Protandrena*	*albitarsis*
Andrenidae	*Calliopsis*	*chlorops*
Andrenidae	*Perdita*	*subgenus "Perdita" 1*
Andrenidae	*Perdita*	*albipennis*
Andrenidae	*Perdita*	*subgenus "Perdita" 2*
Andrenidae	*Protandrena*	*1*
Apidae	*Holcopasites*	*calliopsidis*
Apidae	*Nomada*	*1*
Apidae	*Melissodes*	*4*
Apidae	*Nomada*	*2*
Apidae	*Bombus*	*insularis*
Apidae	*Bombus*	*fervidus*
Apidae	*Bombus*	*pensylvanicus*
Apidae	*Bombus*	*griseocollis*
Apidae	*Bombus*	*nevadensis*
Apidae	*Nomada*	*3*
Apidae	*Bombus*	*huntii*
Apidae	*Ceratina*	*nanula*
Apidae	*Ceratina*	*calcarata*
Apidae	*Ceratina*	*neomexicana*
Apidae	*Nomada*	*5*
Apidae	*Nomada*	*4*
Apidae	*Anthophora*	*urbana*
Apidae	*Nomada*	*6*
Apidae	*Nomada*	*7*
Apidae	*Melissodes*	*6*
Apidae	*Bombus*	*sylvicola*
Apidae	*Melissodes*	*8*
Apidae	*Triepeolus*	*6*
Apidae	*Anthophora*	*terminalis*
Apidae	*Melissodes*	*bimaculata*

Apidae	*Melissodes*	*agilis*
Apidae	*Epeolus*	*bifasciatus*
Apidae	*Diadasia*	*diminuta*
Apidae	*Triepeolus*	*concavus*
Apidae	*Melissodes*	*3*
Apidae	*Melissodes*	*10*
Apidae	*Peponapis*	*pruinosa*
Apidae	*Svastra*	*obliqua*
Apidae	*Melissodes*	*7*
Apidae	*Melissodes*	*5*
Apidae	*Melissodes*	*2*
Apidae	*Bombus*	*occidentalis*
Apidae	*Bombus*	*rufocinctus*
Apidae	*Triepeolus*	*5*
Apidae	*Triepeolus*	*helianthi*
Apidae	*Melissodes*	*1*
Apidae	*Triepeolus*	*1*
Apidae	*Melissodes*	*9*
Apidae	*Triepeolus*	*4*
Apidae	*Melitoma*	*grisella*
Apidae	*Triepeolus*	*remigatus*
Apidae	*Bombus*	*appositus*
Colletidae	*Hylaeus*	*mesillae*
Colletidae	*Hylaeus*	*leptocephalus*
Colletidae	*Hylaeus*	*affinis*
Colletidae	*Hylaeus*	*verticalis*
Colletidae	*Colletes*	*phaceliae*
Colletidae	*Colletes*	*latitarsis*
Halictidae	*Halictus*	*confusus*
Halictidae	*Halictus*	*rubicundus*
Halictidae	*Agapostemon*	*obliquus*
Halictidae	*Halictus*	*ligatus*
Halictidae	*Halictus*	*tripartitus*
Halictidae	*Agapostemon*	*virescens*
Halictidae	*Lasioglossum (Tegulare group)*	*1*
Halictidae	*Lasioglossum (Dialictus)*	*occidentale*
Halictidae	*Lasioglossum (Dialictus)*	*versatum-closest fit*
Halictidae	*Lasioglossum*	*sisymbrii*
Halictidae	*Dieunomia*	*nevadensis bakeri*
Halictidae	*Augochlorella*	*aurata*
Halictidae	*Augochloropsis*	*humeralis*
Halictidae	*Lasioglossum (Dialictus)*	*semicaeruleum*

Halictidae	*Lasioglossum (Dialictus)*	*trigeminum*
Halictidae	*Lasioglossum (Dialictus)*	*albipenne*
Halictidae	*Agapostemon*	*angelicus/texanus*
Halictidae	*Lasioglossum*	*pectoraloides*
Halictidae	*Lasioglossum (Dialictus)*	*anomalum*
Halictidae	*Lasioglossum (Dialictus)*	*imitatum*
Halictidae	*Lasioglossum (Dialictus)*	*pruinosum*
Halictidae	*Agapostemon*	*sericeus*
Halictidae	*Lasioglossum (Dialictus)*	*1*
Halictidae	*Halictus*	*parallelus*
Halictidae	*Agapostemon*	*angelicus*
Halictidae	*Lasioglossum (Dialictus)*	*tenax*
Halictidae	*L. Evylaeus*	*1*
Halictidae	*Lasioglossum (Dialictus)*	*ruidosense*
Halictidae	*Sphecodes*	*1*
Halictidae	*Augochloropsis*	*metallica*
Halictidae	*L. Evylaeus*	*2*
Megachilidae	*Lithurgopsis*	*apicalis*
Megachilidae	*Megachile*	*rotundata*
Megachilidae	*Hoplitis*	*truncata*
Megachilidae	*Hoplitis*	*producta*
Megachilidae	*Megachile*	*frigida*
Megachilidae	*Dianthidium*	*pudicum*
Megachilidae	*Megachile*	*mendica*
Megachilidae	*Megachile*	*centuncularis*
Megachilidae	*Heriades*	*carinata*
Megachilidae	*Megachile*	*perihirta*
Megachilidae	*Anthidium*	*oblongatum*
Megachilidae	*Anthidium*	*manicatum*
Megachilidae	*Coelioxys*	*rufitarsus*
Megachilidae	*Megachile*	*texana*
Megachilidae	*Megachile*	*lippiae*
Megachilidae	*Osmia*	*1*
Megachilidae	*Megachile*	*brevis brevis*
Megachilidae	*Megachile*	*apicalis*
Megachilidae	*Coelioxys*	*octodentata OR novomexicana*
Megachilidae	*Megachile*	*parallela*
Megachilidae	*Hoplitis*	*pilosifrons*
Megachilidae	*Coelioxys*	*1*
Megachilidae	*Megachile*	*montivaga*
Megachilidae	*Osmia*	*2*
Megachilidae	*Stelis*	*lateralis*

Megachilidae	*Megachile*	*latimanus*
Megachilidae	*Osmia*	*coloradensis*
Megachilidae	*Megachile*	*onobrychidis*
Megachilidae	*Osmia*	*3*
Megachilidae	*Stelis*	*1*
Megachilidae	*Megachile*	*mellitarsis*
Megachilidae	*Megachile*	*paralella*
Megachilidae	*Hoplitis*	*fulgida*
Megachilidae	*Osmia*	*4*
Megachilidae	*Hoplitis*	*spoliata*
Megachilidae	*Megachile*	*subexilis*
Megachilidae	*Megachile*	*mellitarsus*
Megachilidae	*Stelis*	*rudbeckiarum*
Megachilidae	*Ashmeadiella*	*bucconis denticulata*
Megachilidae	*Ashmeadiella*	*prosopidis*
Megachilidae	*Coelioxys*	*sayi*
Megachilidae	*Megachile*	*inimica*
Megachilidae	*Megachile*	*fortis*

Table A1.2: Table of butterfly species observed across all Denver parks organized by Family, Genus, Species, and Common Name.

Family	**Genus**	**Species**	**Common Name**
Hesperiidae	*Lon*	*taxiles*	Taxiles Skipper
Hesperiidae	*Polites*	*peckius*	Peck's Skipper
Hesperiidae	*Burnsius*	*communis*	Common Checkered-Skipper
Hesperiidae	*Epargyreus*	*clarus*	Silver-spotted Skipper
Hesperiidae	*Hesperia*	*uncas*	Uncas Skipper
Hesperiidae	*Ochlodes*	*yuma*	Yuma Skipper
Hesperiidae	*Polites*	*themistocles*	Tawny-edged Skipper
Lycaenidae	*Echinargus*	*isola*	Reakirt's Blue
Lycaenidae	*Brephidium*	*exilis*	Western Pygmy-Blue
Lycaenidae	*Strymon*	*melinus*	Gray Hairstreak
Lycaenidae	*Lycaena*	*dione*	Gray Copper
Lycaenidae	*Lycaena*	*heteronea*	Blue Copper
Lycaenidae	*Tharsalea*	*dione*	Gray Copper
Lycaenidae	*Lycaeides*	*melissa*	Melissa Blue
Nymphalidae	*Vanessa*	*atalanta*	Red Admiral
Nymphalidae	*Vanessa*	*cardui*	Painted Lady
Nymphalidae	*Danaus*	*plexippus*	Monarch
Nymphalidae	*Euptoieta*	*claudia*	Variegated Fritillary
Nymphalidae	*Vanessa*	*annabella*	West Coast Lady
Nymphalidae	*Speyeria*	*mormonia*	Mormon Fritillary
Nymphalidae	*Limenitis*	*weiddmeyerii*	Weidemeyer's Admiral
Nymphalidae	*Libytheana*	*carinenta*	American Snout
Nymphalidae	*Vanessa*	*annabella*	West Coast Lady
Nymphalidae	*Junonia*	*coenia*	Common Buckeye
Nymphalidae	*Phyciodes*	*pulchella*	Field Crescent
Nymphalidae	*Euptoieta*	*claudia*	Variegated Fritillary
Nymphalidae	*Polygonia*	*interrogationis*	Question Mark
Nymphalidae	*Junonia*	*grisea*	Gray Buckeye
Papilionidae	*Papilio*	*polyxenes*	Black Swallowtail
Papilionidae	*Papilio*	*rutulus*	Western Tiger Swallowtail
Papilionidae	*Papilio*	*multicaudata*	Two-tailed Swallowtail
Pieridae	*Colias*	*eurytheme*	Orange Sulphur
Pieridae	*Pieris*	*rapae*	Cabbage White
Pieridae	*Colias*	*philodice*	Clouded Sulphur
Pieridae	*Pontia*	*protodice*	Checkered White
Pieridae	*Nathalis*	*iole*	Dainty Sulphur

Table A1.3 Table of floral species observed in Denver parks listed by Latin name, common name, native or non-native status in Colorado, and assigned floral type based on origin and intention of placement. Includes only floral species with pollinator interactions.

Latin Name	**Common Name**	**Origin**	**Floral Type**
Achillea millefolium	Yarrow	Native	Native
Aquilegia coerulea	Colorado blue columbine	Native	Native
Asclepias speciosa	Showy Milkweed	Native	Native
Buddleja davidii	Butterfly-bush	Non-Native	Cultivar
Centaurea cyanus	Cornflower	Non-Native	Cultivar
Centhranthus ruber	Red valerian	Non-Native	Cultivar
Convolvulus arvensis	Field Bindweed	Non-Native	Weedy
Coreopsis lanceolata	Lanceleaf coreopsis	Native	Native
Digitalis purpurea	Common foxglove	Non-Native	Cultivar
Erigeron speciosus	Aspen fleabane	Native	Native
Gaillardia aristata	Common blanketflower	Native	Native
Geranium sanguineum	Bloody geranium	Non-Native	Cultivar
Phedimus aizoon	Sedum aizoon	Non-Native	Cultivar
Ratibida columnifera	Prairie coneflower	Native	Native
Salvia nemorosa	Woodland Sage	Non-Native	Weedy
Salvia pratensis	Meadow sage	Non-Native	Weedy
Sedum spurium	Two-row stonecrop	Non-Native	Cultivar
Stachys byzantina	Lamb's ear	Non-Native	Cultivar
Taraxacum officinale	Common Dandelion	Non-Native	Weedy
Trifolium repens	White Clover	Non-Native	Weedy
Zinnia elegans	Common zinnia	Non-Native	Cultivar
Echinacea purpurea	Purple coneflower	Native	Native
Echinops ritro	Southern globethistle	Non-Native	Cultivar
Gaillardia pulchella	Indian Blanket	Native	Native
Geranium himalayense	Himalayan crane's-bill	Non-Native	Cultivar
Helenium amarum	Bitter sneezeweed	Non-Native	Weedy
Hylotelephium telephium	Orpine	Non-Native	Cultivar
Physostegia virginiana	Obedient plant	Non-Native	Cultivar
Salvia yangii	Russian Sage	Non-Native	Weedy
Sonchus arvensis	Perennial sowthistle	Non-Native	Weedy
Stachys palustris	Marsh woundwort	Non-Native	Weedy
Tagetes erecta	Aztec marigold	Non-Native	Cultivar
Verbascum thapsus	Common mullein	Non-Native	Weedy
Agastache aurantiaca	Orange Hummingbird Mint	Non-Native	Cultivar
Agastache cana	Mosquito plant	Non-Native	Cultivar
Callirhoe involucrata	Purple poppy mallow	Native	Native
Cirsium arvense	Canada thistle	Non-Native	Weedy
Ipomoea alba	Moonflower	Non-Native	Cultivar

Platycodon grandiflorus	Balloon flower	Non-Native	Cultivar
Rudbeckia hirta	Black-eyed Susan	Native	Native
Salvia farinacea	Mealy sage	Non-Native	Weedy
Argemone albiflora	White prickly poppy	Non-Native	Cultivar
Carduus nutans	Nodding thistle	Non-Native	Weedy
Delphinium carolinianum	Carolina larkspur	Native	Native
Erodium cicutarium	Redstem stork's bill	Non-Native	Weedy
Helianthus petiolaris	Prairie Sunflower	Native	Native
Linum lewisii	Lewis flax	Native	Native
Opuntia macrorhiza	Twist spine pricklypear	Native	Native
Rosa arkansana	Prairie Rose	Native	Native
Sisymbrium altissimum	Tall tumblemustard	Non-Native	Weedy
Sphaeralcea coccinea	Scarlet globemallow	Native	Native
Tradescantia occidentalis	Western Spiderwort	Native	Native
Tragopogon dubius	Yellow Salsify	Non-Native	Cultivar
Cleome hassleriana	Spiderflower	Non-Native	Cultivar
Heterotheca villosa	Hairy False Goldenaster	Native	Native
Lupinus sericeus	Silky Lupine	Native	Native
Medicago lupulina	Black Medic	Non-Native	Weedy
Medicago sativa	Alfalfa	Non-Native	Weedy
Melilotus officinalis	Yellow Sweetclover	Non-Native	Weedy
Onopordum acanthium	Scotch thistle	Non-Native	Weedy
Erigeron canadensis	Horseweed	Non-Native	Weedy
Erigeron divergens	Spreading fleabane	Native	Native
Gypsophila paniculata	Baby's breath	Non-Native	Cultivar
Helianthus annuus	Common sunflower	Native	Native
Ipomoea sagittata	Saltmarsh morning-glory	Non-Native	Cultivar
Liatris punctata	Dotted Gayfeather	Native	Native
Solanum angustifolium	Buffalo bur	Non-Native	Cultivar
Solidago canadensis	Canada goldenrod	Native	Native
Dalea purpurea	Purple Praire Clover	Native	Native
Gazania rigens	Treasure Flower	Non-Native	Cultivar
Heliopsis helianthoides	False sunflower	Native	Native
Penstemon strictus	Rocky Mountain Penstemon	Native	Native
Rosa chinensis	China rose	Non-Native	Cultivar
Asclepias incarnata	Swamp milkweed	Native	Native
Chamaebatiaria millefolium	Desert sweet	Native	Native
Hemerocallis fulva	Ditch lily	Non-Native	Cultivar
Leucanthemum vulgare	Oxeye daisy	Non-Native	Cultivar
Monarda fistulosa	Wild bergamot	Native	Native
Symphoricarpos occidentalis	Western snowberry	Native	Native
Vernonia fasciculata	Western ironweed	Native	Native

Veronica longifolia	Garden speedwell	Non-Native	Cultivar
Ericameria nauseosa	Rubber rabbitbrush	Native	Native
Eutrochium maculatum	Spotted Joe-Pye weed	Native	Native
Liatris spicata	Dense Blazing star	Non-Native	Cultivar
Limonium carolinianum	Lavender thrift	Non-Native	Cultivar
Plumbago auriculata	Cape leadwort	Non-Native	Cultivar
Solidago rigida	Stiff goldenrod	Native	Native
Malva neglecta	Common Mallow	Non-Native	Cultivar
Verbena bracteata	Bigbract verbena	Native	Native
Berlandiera lyrata	Chocolate flower	Native	Native
Crataegus pinnatifida	Mountain Hawthorn	Non-Native	Cultivar
Gomphrena globosa	Globe Amaranth	Non-Native	Cultivar
Penstemon digitalis	Foxglove beardtongue	Non-Native	Cultivar
Penstemon heterophyllus	Bunchleaf penstemon	Non-Native	Cultivar
Petunia atkinsiana	Garden petunia	Non-Native	Cultivar
Rosa hybrida	Hybrid tea rose	Non-Native	Cultivar
Salvia greggii	Autumn sage	Non-Native	Cultivar
Caryopteris mongholica	Bluebeard	Non-Native	Cultivar
Eryngium alpinum	Alpine sea holly	Non-Native	Cultivar
Allium cernuum	Nodding onion	Native	Native
Achillea filipendulina	Fern-leaf yarrow	Non-Native	Cultivar
Allium giganteum	Giant onion	Non-Native	Cultivar
Amsonia tabernaemontana	Eastern bluestar	Non-Native	Cultivar
Baptisia australis	Blue wild indigo	Native	Native
Baptisia sphaerocarpa	Yellow wild indigo	Non-Native	Cultivar
Echinacea paradoxa	Yellow coneflower	Non-Native	Cultivar
Papaver rhoeas	Common poppy	Non-Native	Cultivar
Stanleya pinnata	Desert princesplume	Native	Native
Centaurea macrocephala	Giant Knapweed	Non-Native	Cultivar
Nepeta cataria	Catnip	Non-Native	Weedy
Salvia splendens	Scarlet sage	Non-Native	Cultivar
Cleome serrulata	Rocky Mountain Beeplant	Native	Native
Coreopsis tinctoria	Plains coreopsis	Native	Native
Eutrochium purpureum	Purple Joe-Pye weed	Native	Native
Penstemon centranthifolius	Scarlet bugler	Non-Native	Cultivar
Visnaga daucoides	False queen anne's lace	Non-Native	Cultivar
Lobularia maritima	Sweet alyssum	Native	Native
Ageratum houstonianum	Flossflower	Non-Native	Cultivar
Antirrhinum majus	Snapdragon	Non-Native	Cultivar
Dianthus barbatus	Sweet William	Non-Native	Cultivar
Heliotropium arborescens	Cherry pie plant	Non-Native	Cultivar
Galinsoga quadriradiata	Shaggy soldier	Non-Native	Weedy

Tithonia diversifolia	Mexican sunflower	Non-Native	Cultivar
Zinnia angustifolia	Creeping zinnia	Non-Native	Cultivar
Phedimus spurius	Caucasian stonecrop	Non-Native	Cultivar
Sedum lineare	Needle stonecrop	Non-Native	Cultivar
Veronica spicata	Spiked speedwell	Non-Native	Cultivar
Melilotus albus	White Sweetclover	Non-Native	Weedy
Grindelia squarrosa	Curlycup gumweed	Native	Native
Machaeranthera tanacetifolia	Tansyleaf Tansyaster	Native	Native
Trifolium pratense	Red Clover	Non-Native	Weedy
Amblyolepis setigera	Huisache daisy	Non-Native	Cultivar
Asclepias tuberosa	Butterfly weed	Native	Native
Coreopsis verticillata	Threadleaf coreopsis	Non-Native	Cultivar
Symphyotrichum lanceolatum	White-panicle aster	Native	Native
Achillea tomentosa	Woolly Yarrow	Native	Native
Descurainia pinnata	Tansymustard	Native	Native
Glycyrrhiza lepidota	American Licorice	Native	Native
Eryngium yuccifolium	Rattlesnake master	Non-Native	Cultivar
Cornus sericea	Red-osier Dogwood	Native	Native
Linaria dalmatica	Dalmation Toadflax	Non-Native	Cultivar
Cosmos bipinnatus	Garden Cosmos	Native	Native
Lactuca serriola	Prickly lettuce	Non-Native	Weedy
Salix exigua	Narrowleaf willow	Non-Native	Weedy
Astragalus cicer	Chickpea milkvetch	Non-Native	Weedy
Geum rivale	Water avens	Native	Native
Penstemon palmeri	Penstemon palmeri	Native	Native
Lupinus arboreus	Yellow Bush Lupine	Non-Native	Cultivar
Erigeron annuus	Daisy Fleabane	Non-Native	Weedy
Lythrum salicaria	Purple loosestrife	Non-Native	Weedy
Solidago juncea	Early goldenrod	Non-Native	Weedy
Origanum vulgare	Oregano	Non-Native	Weedy

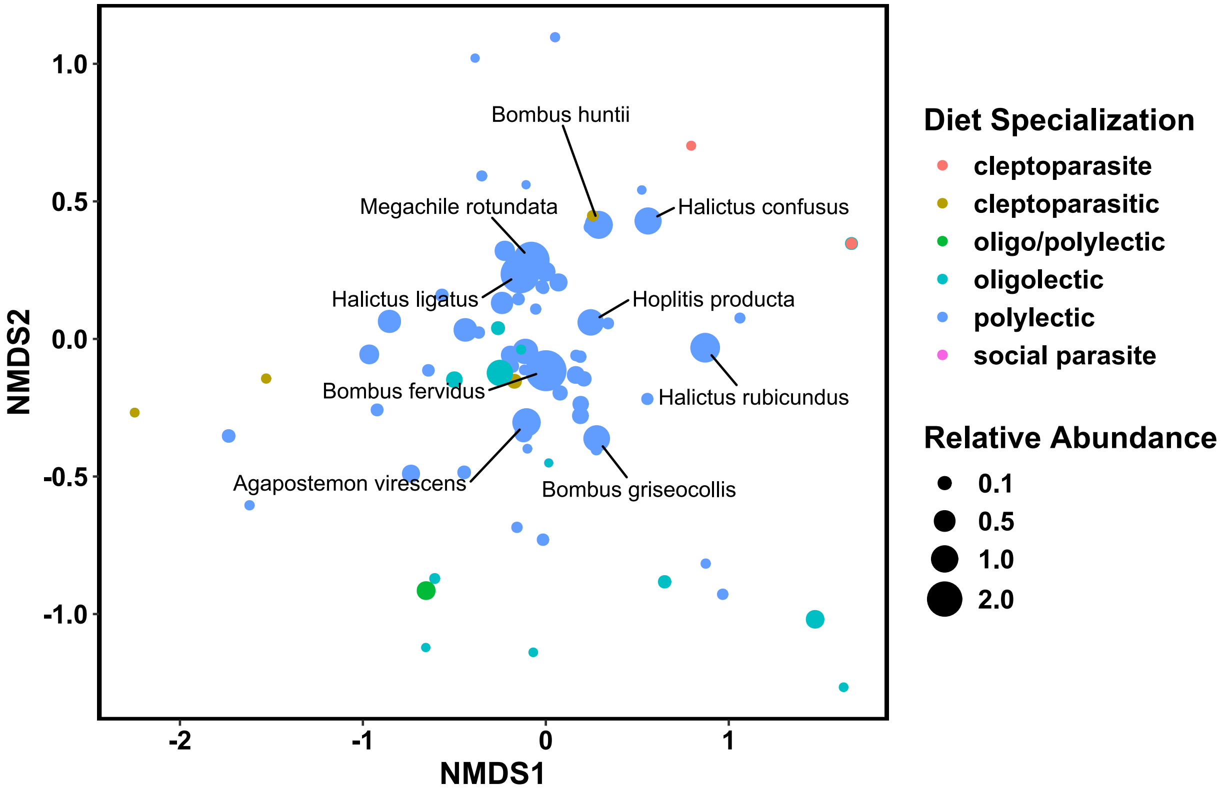

Figure A1.1 Non-metric multidimensional scaling (nMDS) plot based on Bray-Curtis dissimilarity for wild bee relative abundances for each species recorded in the Denver Parks, showing that the most often observed species represented by the largest circles were all generalist foragers. The less frequently observed species often fell into other diet specialization groups. The top 10% most abundant wild bees are labeled by Latin name.